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The *Homo habilis* Paradox: Is *Homo habilis* an Australopithecine Moonlighting as the First Migrant Out of Africa?

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Introduction

When Bed I of the Olduvai Gorge was excavated in 1959, hominid remains were recovered that would revolutionize the field of paleoanthropology. Oldowan tools associated with the fossils prompted researchers to name this new species *Homo habilis*, the 'handyman', and to position it at the base of the human genus (Leakey et al. 1964). However, recent articles forwarded by Wood and Collard (1999a, 1999b) challenge this hominid's traditional taxonomic position by re-assigning it to the genus *Australopithecus*. The unrelated, but equally important, discoveries of the Dmanisi and Longgupo hominids propel interpretations of *Homo habilis* in a different direction. These findings introduce the possibility that a group of habiline migrants formed the first expansion out of Africa (Gabunia et al. 2002, Wanpo et al. 1995). Certainly the literature presents an interesting paradox: is *Homo habilis* primitive enough to be classified as an australopithecine, or advanced enough to colonize Eurasia? In an endeavour to clarify *Homo habilis*' evolutionary role, this paper will explore recent amendments to its conventional phylogenic position. The plausible classification of the Dmanisi and Longgupo remains will be discussed, along with their implications for hominid migratory models. Finally, this paper will attempt to reconcile the *Homo habilis* paradox by proposing taxonomic revisions and identifying a new subspecies: *Homo habilis transmigro.*

Literary Review: Old Assumptions and New Discoveries

Homo habilis' membership within genus *Homo* is based upon a number of putative features such as a 600 cubic centimetre cranium, a capacity for language, precision grip, and a habitual bipedal gait (Wood & Collard 1999a:198). Traditionally, this hominid was considered to be the basal species of a single lineage that gradually evolved into anatomically modern *Homo sapiens* (Conroy 2005:302). Yet in the 1970s, fossils found at the Koobi Fora Formation in Kenya presented a major difficulty for the long-standing notion of anagenesis. Though initially identified as early *Homo habilis*, subsequent comparative studies exposed a great deal of variation between these specimens and the Olduvai sample. The divergences between the two skeletal assemblages, found particularly in the postcranial and craniodental complexes, are so marked that a new species was established to accommodate some of the Koobi Fora hominids: *Homo rudolfensis* (Conroy 2005:315-318).

Since the 2001 description of *Kenyanthropus platyops*, many paleoanthropologists support the reassignment of *Homo rudolfensis* to this autonomous evolutionary lineage (Leakey et al 2001:439, Lieberman 2001:419-420, Tattersall 2003). Nevertheless, this revision does not spell the end for a 'bushier-looking' cladogram of the genus *Homo*. Numerous Plio-Pleistocene sites

continue to produce evidence of multiple contemporaneous species dispersed across Africa and Eurasia. Most researchers now agree that the morphological diversity represented by the post-australopithecine sample is too great to be contained by a single species (Brown et al. 2004, Lahr & Foley 2004, Tattersall 2003). Indeed, the rejection of anagenetic models also calls into question *Homo habilis*' comfortable position at the base of its genus.

In 1999, Wood and Collard presented a new interpretation of *Homo habilis*' morphology that removed this species from the human lineage entirely. They argued that the traditional criteria for admission into the genus *Homo* are arbitrary, and confuse the boundary between highly-evolved hominids and the ancestral australopithecines (Wood and Collard 1999a:199-200, 1999b:65-66). When *Homo habilis* was first described in the 1960s, the minimum cranial capacity for the genus *Homo* was set at 600 cubic centimetres. The biological significance of this brain size is questionable, especially since Leakey *et al.* (1964) adjusted the original parameter in order to position their Olduvai habilines at the base of the human line (Wood & Collard 1999a:199 and 1999b:66). Furthermore, endocranial casts do not produce reliable representations of the brain's linguistic areas; so *Homo habilis*' possession of language is also debatable (Wood & Collard 1999b:66). Even the species' 'handyman' status is challenged by the possibility that a contemporaneous and dexterous australopithecine may have produced Oldowan tools (Wood & Collard 1999b:66).

In light of these classificatory shortcomings, Wood and Collard offered new minimum requirements for admittance into the *Homo sapiens* lineage. They argued that a hominid group belongs within the genus *Homo* when it exhibits a human-like body size, body shape, brain size, ontogeny, and masticatory apparatus (Wood & Collard 1999b:67-70). These physical characteristics are relevant to taxonomy because they indicate that the species also shares *Homo sapiens'* adaptive strategies (Wood & Collard 1999b:70). Conversely, a fossil taxon will diverge from this paradigm when it occupies a different eco-niche and belongs to a separate evolutionary line. According to Wood and Collard's (1999b:67-70) study, *Homo habilis* falls short of the new criteria on every count, save brain size. They observed that *Homo habilis* more closely approximates the australopithecine pattern and would be better accommodated by the genus *Australopithecus* (Wood & Collard 1999b:70). Though their research makes a good case for the re-assignment of habilines, primitive fossils found outside of Africa suggest that this revision is premature.

Located at the southern border of the Republic of Georgia, the Dmanisi site has yielded hominid remains that raise questions about the validity of Wood and Collard's criteria. Archaeologists excavating a medieval village uncovered ancient craniofacial fragments within the floor of a historic building's cellar. Stone tools affiliated with the fossils more closely resemble simple Oldowan implements than the complex Acheulian hand axes of African and European *Homo erectus sensu lato* (Gabunia et al. 2001:164, Vekua et al. 2002:86, Swisher *et al.* 1994:1121). Relative dating established a reliable age of 1.75 million years, which signifies that these hominids lived

contemporaneously with several Javanese populations of *Homo erectus* (Swisher et al. 1994:1118, Gibbons 1994:1087, Vekua et al. 2002:85). Although these two ancient populations share a continent and a very early timeframe, they differ noticeably in terms of their gross morphology. The Dmanisi specimens have substantially smaller cranial capacities than Asian *Homo erectus* and exhibit a number of craniofacial features that correspond to the *Homo habilis* pattern (Rightmire et al. 2006:115, Vekua et al. 2002:85 and 88). Despite these primitive retentions, the fossils share a number of derived traits with the Javanese groups.

Fragmentary faciocranial remains recovered from the Longgupo Cave in central China also exhibit a unique combination of primitive and derived characteristics. One hundred and sixteen associated faunal specimens secured a relative date range of 1.96 to 1.78 million years. Wood and Turner (1995:240) observed that the scanty sample of fractured hominid bones offers 'meager pickings' for taxonomic assignment; however, a lower premolar (Pm_4) embedded within a piece of mandible is diagnostic. This tooth, found alongside an assemblage of Oldowan-like tools, provides additional evidence for the colonization of Asia by a habiline. In fact, the age and location of the fossils suggest that these hominids formed the initial migratory wave through the Levantine corridor approximately two million years ago (Wanpo et al. 1995:278).

The early dates and primitive morphology of the Dmanisi and Longgupo fossils came as a major surprise to the field of paleoanthropology. Since trans-continental travel requires a hominid to possess human-like adaptive strategies, the first pioneers out of Africa were assumed to have had a human-like morphology. In fact, this presumption is the very crux of Wood and Collard's argument for the taxonomic revision of genus *Homo*. The primitive-looking bones, teeth, and tools from the two Asian sites conflict with their revisions to the criteria for a species' admittance into the human genus. These assemblages prove that small-brained hominids with underdeveloped masticatory complexes and simple toolkits were capable of occupying a *Homo sapiens*-like eco-niche. In a similar fashion, *Homo habilis*' primitive retentions do not necessarily exclude it from the behavioural ecology of archaic *Homo*. In addition to contradicting Wood and Collard's major conclusions, the Dmanisi and Longgupo fossils also present problems for *Homo erectus*' long-established title as the 'first migrant' out of Africa.

Some researchers have reconciled the existence of these anomalous fossils by representing them as an early grade of *Homo erectus sensu lato* (Gabunia et al. 2001, Lordkipanidze et al. 2006, Rightmire et al. 2006). However, such interpretations are often biased by personal beliefs about the splitting or lumping of African and Asian *Homo erectus*. For the sake of clarity, this paper will employ the taxonomic splitter's nomenclature when referring to these species; whereby, the term *Homo ergaster* refers to African specimens and *Homo erectus* designates Asian specimens (Schwartz 2004). The Dmanisi craniofacial remains share a significant number of *Homo erectus* and *Homo ergaster*-like traits: an elevated nasal saddle, a bar-like supraorbital torus on the parietals, a low temporal squama with a straight upper border passing downward

toward asterion, flexion of the occiput, and a constricted foramen lacerum (Lordkipanidze et al. 2006:1156). Gabunia et al. (2001:165, Fig. 1) argued that the recently-discovered D2280 and D2282 crania affiliate the Dmanisi population with East African *Homo ergaster*. The D2280 and D2282 specimens possess characteristics that distinguish them from Asian *Homo erectus;* such as their tall, thin-walled, and long cranial vaults, their moderate-sized supraorbital tori, and aspects of their lower dentition (Gabunia et al. 2001:165-166). Yet, those who are eager to lump the Dmanisi assemblage with *Homo ergaster* must first explain the small number of synapomorphies it shares with the Javanese *Homo erectus* sample (Conroy 2005:417, Lordkipanidze et al. 2006:1156). To add to the classificatory confusion, Vekua et al. (2002:85) noted that "the Dmanisi specimens are the most primitive and small-brained fossils to be grouped with [*Homo ergaster*]". In sum, these crania most closely resemble *Homo ergaster*, but also incorporate several *Homo erectus* specializations and some primitive habiline retentions. The traits that approximate the *Homo habilis* pattern are often represented as plesiomorphies, which situate the Dmanisi and Longgupo hominids at the stem of the *Homo ergaster* species (Lordkipanidze et al. 2006:1156, Rightmire et al. 2006:139).

Researchers who readily dismiss the Dmanisi hominids' habiline features run the risk of misinterpreting the significance of these primitive retentions. If the fossil crania truly represent an early form of *Homo ergaster*, there should be some degree of brain size continuity between the two groups. However, the upper range of the Dmanisi cranial capacities generally falls short of the lower size limit for *Homo ergaster* (Rightmire et al. 2006:139). Paleoanthropologists are hard-pressed to explain why the ancestral, smaller-brained hominids appear in the archaeological record *after* their larger-brained African descendents. Moreover, *Homo erectus* has a relatively specialized morphology; yet, somehow this species co-existed with its unsophisticated 'ancestor'. Based on affinities in brain size and certain craniofacial features, Gabunia et al. (2002:88, Fig. 2) remarked that "it can be argued that [the Dmanisi] population is closely related to *Homo habilis"*. Hopefully, the Dmanisi site will produce well-preserved long bones that will clarify the phylogenetic relationship between these hominids and other species of *Homo* (Balter & Gibbons 2002).

Figure 1: Lateral views of D2280 (right) and D2282 (left) crania, from Dmanisi Site (Rightmire et al. 2006:118).

Figure 2: Lateral views of D2700 (right) and KNM-ER 1813 (left). The Dmanisi subadult is slightly larger than the Koobi Fora [*H. habilis*], but the crania are similar in midfacial profile, supraorbital development and rounding of the occiput. (Rightmire et al. 2006:127)

In contrast to 'lumping' the Dmanisi crania within *Homo ergaster* or *Homo habilis* hypodigms, some scientists entertain the possibility that this assemblage actually represents two species. In the year 2000, an archaeological team unearthed mandible D2600, which is considerably larger than all other local specimens (Gabunia et al. 2002). Those studying the fossil initially hypothesized that its unique dimensions corresponded to a new species, *Homo georgicus*, which may have lived alongside a migrant group of *Homo ergaster* (Gabunia et al. 2002:243). However, a comparison between the gracile D211 mandible and the robust D2600 specimen could not rule out the possibility that this hominid population expressed extreme sexual dimorphism (Gabunia et al. 2002:244). Thus, the researchers concluded that the Dmanisi site was occupied by only *Homo georgicus* (de Lumley & Lordkipanidze 2006, Gabunia et al. 2002:244-245). This proposition has not gained support in the literature (Balter & Gibbons 2002). One outlying individual does not substantiate the creation of a new species, especially since the rest of the specimens at the site are morphologically affiliated with African members of genus *Homo*.

In addition to presenting paleoanthropologists with a taxonomic conundrum, the Dmanisi and Longgupo remains also defy traditional assumptions about early hominid migration. Clearly, *Homo erectus*' momentous departure from Africa, approximately one million years ago, is no longer a tenable scenario. If the primitive fossils from the two new Asian sites represent a taxon other than *Homo ergaster*, be it *Homo habilis* or *Homo georgicus*, then they signify that trans-continental movements were undertaken by multiple species (de Lumley & Lordkipanidze 2006, Gabunia et al. 2002, Schwartz et al. 2000). Furthermore, the habiline-like cranial capacities of the Dmanisi specimens violate the popular notion that early *Homo* required a relatively large brain to migrate northwards (Vekua et al. 2002). Their diminutive crania also indicate that the Dmanisi hominids were correspondingly small-bodied. Since the fossils retain a number of habiline craniofacial features, it is likely that they also possess *Homo habilis*-like limb proportions. Unfortunately, the Dmanisi site has not produced enough postcranial material to confirm this speculation. Future long bone discoveries will ultimately support or reject the supposition that short legs physically prevented early hominids from traveling long distances (Balter & Gibbons 2002).

Material culture from the Dmanisi and Longgupo site abolishes many preconceptions about the first pioneers into Eurasia. Acheulian implements are no longer considered to be the breakthrough technology that facilitated hominid expansion into new eco-niches. The 1.8 million-year-old Javanese assemblages show that the earliest *Homo erectus* populations were capable of migrating without the help of hand axes (Gibbons 1994). In fact, the lithic artifacts from the Dmanisi and Longgupo sites demonstrate that the first trans-continental travelers were fabricators of simplistic Oldowan tools (Wanpo et al. 1995). Gowlett (2006:299) wondered how such small-brained members of early *Homo*, equipped with the most basic technology, were capable of inhabiting temperate regions. He argued these primitive hominids were not hardy enough to

cope with Pleistocene climatic changes without assistance (Gowlett 2006:299).

Thus, Gowlett (2006:304) proposed that adverse environmental conditions created selective pressure for the innovation of new tools, such as the controlled use of fire. This conjecture is too far-reaching, since it suggests that the first colonizers of Eurasia possessed fire technology long before the African hominids did. Indeed, the best-known evidence of fire use prior to one million years ago is derived from the Swartkrans, Koobi Fora, and Chesowanja sites. The hominid who originally wielded this technology has yet to be identified (Conroy 2005:302). The Asian archaeological record demonstrates that *Homo erectus* began to employ fire as late as the middle Pleistocene. Conversely, the Dmanisi and Longgupo sites do not offer a single trace of empirical support for Gowlett's (2006) claim. He blamed this lack of evidence on the fact that the negligible population densities of this time equate to a very low probability that ancient campfires will ever be sampled (Gowlett 2006:305). This argument is also problematic because the Dmanisi site is known for its excellent preservation of delicate skeletal material. Archaeologists have uncovered dozens of hominid specimens and innumerable faunal remains; therefore, it seems unlikely that burnt bone fragments and charcoal deposits would completely escape detection. Nevertheless, if Gowlett's (2006) speculations are correct, paleoanthropologists must revise their assumptions about the origins of fire use. Early migrants with access to this technology would have adapted to their new territory in ways that approximate the human pattern, like withstanding colder temperatures and cooking their food. The discovery of additional ancient sites will hopefully clarify the ambiguous issue of Eurasian fire use.

Discussion

Clearly, the fundamental tenets of the traditional *Homo erectus* migration model fail to accommodate the Dmanisi and Longgupo specimens; thus, researchers are required to formulate alternate hypotheses. Those who assign these fossils to the base of the *Homo ergaster* clade suggest that this species expanded into Eurasia shortly after its appearance in Africa (Gabunia et al. 2001, Potts et al. 2004). *Homo erectus* evolved from the groups that remained in their ancestral continent, and formed a second wave of northward migration. The geographic and genetic isolation of the Dmanisi pioneers explain the apomorphic features of the crania. Although these hominids are not unique enough to be split into their own species, *Homo georgicus*, Rightmire *et al.* (2006:140) believe that they merit the designation of a new *Homo erectus (sensu lato)* subspecies.

However, a major problem with this hypothesis relates to the synapomorphies shared between the Dmanisi fossils and the derived groups of Asian *Homo erectus*. Classifying these hominids as stem-grade *Homo ergaster* precludes the possibility that this population could acquire such specializations. Parallel evolution cannot explain the presence of these derived features, since the migrants were exploiting ecological zones unlike those of Africa. Therefore, Dmanisi and Longgupo fossils are unlikely candidates for a taxonomic position at the base of the *Homo ergaster* clade.

Several recently redated Javanese sites have generated a new perspective on hominid migration that drastically diverges from traditional models. Rightmire et al. (2006:140) observed that, "dating does not presently rule out the possibility that *H. erectus* [*sensu lato*] originated in Eurasia and that some groups then returned to Africa, where they evolved toward *H. erectus ergaster*". In other words, habiline migrants passed though the Levantine corridor to establish Indonesian populations of *Homo erectus*, which later spread back into their ancestral continent. For this scenario to work, the derived form of Asian *Homo erectus* must have evolved spontaneously from the contemporaneous Dmanisi and Longgupo groups. Furthermore, this 'lumper' interpretation requires several evolutionary reversals to occur, since the generalized African communities of *Homo erectus* were supposedly founded by more specialized members of their species.

On the other hand, taxonomic 'splitters' maintain the view that Eurasia was first colonized by a stem-grade of *Homo ergaster* (Wood & Turner 1995). These isolated populations later evolved into the separate *Homo erectus* clade, while their African ancestors maintained their phylogenetic integrity. Once again, the contemporaneity of the Dmanisi and Java hominids presents theoretical difficulties. The numerous morphological disparities between the crania from the two sites reveal the implausibility that *Homo erectus* arose directly from such a primitive-looking ancestor.

Surely, there must be a more parsimonious alternative to such inadequate migratory models. The small brain sizes and primitive craniofacial features of the Dmanisi specimens preclude an affiliation with the more highly-evolved *Homo erectus* and *Homo ergaster* species. Hence, these hominids are derived from an earlier member of the genus *Homo*. Out of consideration for Wood and Collard's (1999a, 1999b) recent taxonomic revisions, this paper will refer to this ancestral taxon as 'proto-habiline'. Proto-habilines were likely the earliest members of the human genus; however, there remains a possibility that this species was actually a late grade of *Australopithecus*. Just before *Homo ergaster* split from the proto-habiline lineage to form its own autonomous species, a group of hominids left Africa to establish the Dmanisi and Longgupo sites. For this reason, the pioneers of Asia retain habiline traits but also exhibit *Homo ergaster* synapomorphies. The newly-established colonies became reproductively isolated and no longer contributed to the human line. Geographic seclusion and cranial apomorphies suggest that the Dmanisi hominids are better described as a subspecies of *Homo habilis*. Therefore, this paper proposes the tentative name *Homo habilis transmigro*: the 'migrating handyman' (Fig. 3). More skeletal material from the Longgupo site is required in order to affiliate its prehistoric occupants within this new category. Meanwhile, the populations that remained in Africa proceeded to diverge into two separate taxa: *Homo ergaster* and *Homo habilis*. African *Homo ergaster* formed a second hominid pulse into Eurasia, which ultimately evolved into the erectines that first appeared in Java. The Indonesian and Dmanisi taxa experienced similar environmental pressures, so any cranial synapomorphies they share would have been the result of parallel evolution.

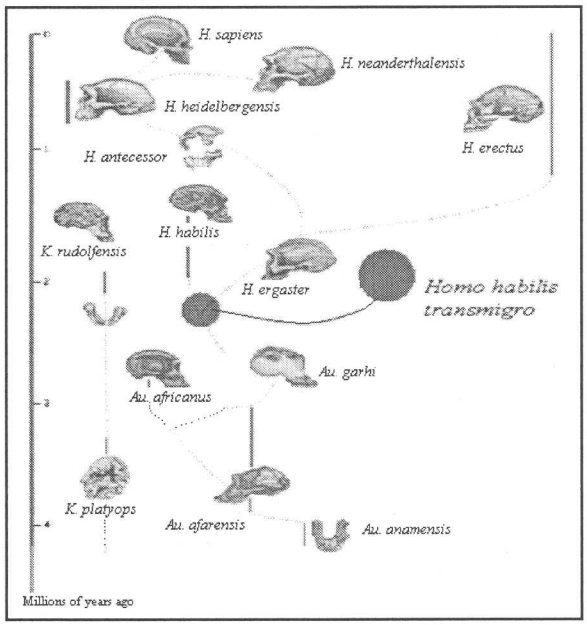

Figure 3: Adapted from Tattersall's (2003) phylogeny

Conclusions

Ultimately, the *Homo habilis* paradox may be resolved by major revisions to hominid migratory models and taxonomy. Contrary to Wood and Collard's (1999a, 1999b) arguments, *Homo habilis* is not primitive enough to be classified as an australopithecine, as evidenced by their ability to travel across continents and colonize strange lands. These achievements approximate *Homo sapiens'* adaptive strategies and firmly establish this taxon at the base of the human line. The Dmanisi and Longgupo fossils present paleoanthropologists with a classificatory nightmare. However, their unique combination of primitive and derived traits is best accommodated by a new subspecies category: *Homo habilis transmigro*. The recognition of Asian habilines challenges many traditional presumptions about the first hominid migration out of Africa. Additional long bone and cranial material from the Dmanisi and Longgupo sites will confirm or deny the existence of multiple, contemporaneous taxa co-existing throughout ancient Eurasia.

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